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Recurrent selection for broad adaptation affects stability of oat

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Summary

A recurrent selection program for adaptation to diverse environments was successful in improving mean oat (*Avena sativa* L.) grain yield within and across testing environments. The objectives of this research were to determine if this selection program also resulted in changes in other agronomic traits or altered yield stability. Additionally, we investigated how selection modified the response of genotypes to climatic conditions. We evaluated random samples of 100 families from the original population and each of three selection cycle populations in replicated yield trials in Idaho, Iowa, and Norway for two years. Yield stability was assessed via joint regression analysis and superiority analysis. For each cycle, genetic relationships among yields observed in different environments were assessed by estimating phenotypic correlations between pairs of target environments. The effect of climate variables on genotype-by-environment interaction (GEI) responses was determined with partial least squares regression. Selection resulted in a small increase in mean heading date, a decrease in mean test weight, and no change in total above-ground biomass or plant height. Genotypic regression coefficients on environmental indices and deviations from regression were larger in the last cycle population, but superiority analysis demonstrated that selection significantly improved the adaptability of the population to the target testing environments. Improved adaptation was also demonstrated by increased phenotypic correlations among the most divergent pairs of environments in the later cycles. Partial least squares regression of GEI effects on climate variables suggested that later cycle families tended to respond more favorably to cooler than average conditions than the original population. Selection resulted in improved yield stability as well as improved mean yield.

Abbreviations: AMMI – additive main effects and multiplicative interactions; GEI – genotype-by-environment interaction

Introduction

Oat grain yield is strongly influenced by environmental conditions, with the result that oat yields often fluctuate greatly from year to year. Improving the dynamic stability (as defined by Becker & Leon, 1988) of oat yields in target production environments is an important breeding objective. Unfortunately, a tradeoff between mean productivity and stability often exists. Selection on the basis of yield stability frequently is predicted to result in lower mean yields (Finlay & Wilkinson, 1963; Helms, 1993). Conversely, selection for greater mean yield may result in lower stability (Simmonds, 1991).

Holland et al. (2000) reported that recurrent selection for broad adaptation to diverse environments in oat resulted in significant increases in mean population grain yield both within and across environments. In addition, the mean genetic correlation among yields in different environments increased, suggesting that

yield stability across environments also increased in later cycles of selection. A better understanding of the changes in stability or adaptability due to selection in the oat population described by Holland et al. (2000) would be achieved through the comparison of selection cycles based on a variety of stability measurements and by estimating the correlated responses to selection in variables that may affect adaptability. Whereas many previous studies have investigated stability of selected cultivars or lines representing one stage of a breeding program, the experiment described in Holland et al. (2000) represents an opportunity to investigate the changes in mean genotypic performance and genotype-by-environment interaction effects among different cycles of a breeding program designed to improve adaptability across diverse environments.

Stability parameters of interest include the Eberhart-Russell regression coefficient (b_i) and Lin & Binns' superiority parameter (P_i). Eberhart & Rusell's (1966) parameter is based on the regression of each line's yield on the environmental index (the mean yield at each environment). According to Eberhart & Rusell (1966), a stable line has unity regression coefficient, minimum deviation from regression, and high mean yield. Lin & Binns' (1988) superiority parameter (P_i) is the squared difference between the line's yield and the maximum yield within each environment, averaged over all environments. Genotypes with broader adaptation have lower values of this superiority parameter, because they yield closer to the maximum yield within each environment, relative to genotypes with poorer adaptation to the target set of environments.

Holland et al. (2000) reported that the mean genetic correlation among environments increased due to selection for broad adaptation in their oat population. This indicated that genotypic responses to different test environments were more predictable in later cycles. Cooper and DeLacy (1994) suggested that, when genotype by environment interaction is important, the individual correlations between pairs of test environments that compose the mean correlation among all test environments is of interest. Phenotypic correlations between pairs of environments indicate the nature and magnitude of indirect responses if selection is conducted in one environment and evaluated in a second environment (Cooper & DeLacy, 1994). Furthermore, some pairs of environments may be negatively correlated, but such cases will not be revealed unless the individual environment pair correlations are estimated, because the mean genotypic correlation among environments is expected to be greater than or equal to zero.

An alternative, and complementary, method of evaluating relationships among environments is through multivariate analysis of genotype-by-environment interactions (Crossa, 1990; Lin et al., 1986). Additive main effects and multiplicative interactions (AMMI) analysis has been used to partition the genotype-by-environment interaction (GEI) effects (remaining after accounting for environment and genotype main effects from multi-environment yield trial data) with a principal components analysis (Crossa, 1990; Gauch, 1992). Differences in stability and adaptability among genotypes are then evaluated qualitatively based on graphical displays. In addition, relationships among testing environments can be revealed by plotting the environments according to their principal component scores from the AMMI analysis. We propose to investigate the nature of changes in genotypic responses to test environments brought about by selection by first employing this descriptive method of grouping environments according to similar GEI responses. These descriptive relationships can then guide interpretation of the observed phenotypic correlations between pairs of environments.

Finally, the influence of climate variables on GEI effects in the different cycles of selection can be compared to determine if selection has altered the mean genotypic response to specific climate variables. This comparison can be made by regressing the GEI effects on climate variables measured in each environment using partial least squares regression (Aastveit & Martens, 1986; Vargas et al., 1998). Partial least squares regression relates one or more factors that represent much of the variation in the causal climate variables to factors that explain much of the GEI variance (similar to the principal components of the AMMI analysis). Differences among cycles' interactions with environments then can be related to their reactions to climate variables estimated using partial least squares regression.

The objectives of this research were to determine if selection for greater grain yield in divergent environments resulted in changes in means of other agronomically important traits, yield stability (measured using regression on environmental indices and superiority statistics), correlations among pairs of environments, or interactions between genotypes and specific climate variables.

Materials and methods

Population development and recurrent selection

Population development and selection procedures were described in detail by Holland et al. (2000). Briefly, a broad-based population was developed from crosses among 20 oat cultivars and experimental lines from U.S.A., Canada, Norway, and Sweden. Full-sib families in the S1 generation were developed from the base (C0) population and tested in replicated hill plot trials in three Iowa locations (near Ames, near Kanawha, and near Nashua), Aberdeen, ID; and Kapp, Norway. Families that yielded well in all environments were selected and intermated at random to form a new population (C1). Full-sib families in the S1 generation were also developed from the C1 population and evaluated in the same way as the C0 population. Selection and intermating were repeated for three cycles of selection. Details of the selection method varied slightly among cycles, but a positive selection differential was maintained within each site for each cycle (Holland et al., 2000). Population sizes ranged from 190 to 250 full-sib families each cycle. Percentages of population selected ranged from 16% to 26% each cycle. The Norwegian testing site was changed to Ås, Norway for C2 and later evaluations.

Evaluation experiment

Details of the evaluation experiment were given by Holland et al. (2000). To summarize, random samples of 210 full-sib families from C3, 100 full-sib families from each other cycle population (C0-C2), and the 20 original parental lines were selected for testing. Entries from C0-C3 were randomly assigned to four sets, such that each set contained all 20 original parents; 25 full-sib families from C0, C1, and C2; and 52 or 53 full-sib families from C3. Some parental lines were duplicated in sets to make 156 entries per set. A sets within replications design was used, and the entries within sets were arranged in 12 x 13 triple lattices at each location (Ås, Aberdeen, Ames, Kanawha, and Nashua). In 1996, the same entries were used, except that only 100 randomly-chosen C3 families were included, plus one C3 family, IA94366, that was selected as a check line based on its outstanding yield performance in 1995, and there were 132 entries per set. A sets within replications design was used, and the entries were arranged in 11 $\times$ 12 triple lattices at each of the same five locations.

Grain yields were measured on every plot in each environment and adjusted for percentage of hulless grain as described by Holland et al. (2000). Heading dates and plant heights were measured on every plot at Ås, Aberdeen, and Ames. Above-ground biomass was measured on every plot at Ås (1995 only) and Ames, Kanawha, and Nashua. Grain test weight was measured on samples of grain bulked over replications for each entry in each environment.

Statistical analyses

Each set within each environment was analyzed separately, and entry means adjusted for lattice block effects were obtained using SAS Proc MIXED (SAS Institute Inc., 1999). Means across the three Iowa locations within each year were computed to estimate an Iowa mean for each set. Means over years were computed for Ås, Aberdeen, and Iowa locations, including for C3 only those families tested in both years. Means over years and locations (considering the Iowa mean from each year as a single-location mean) were computed for each set. Finally, the cycle population means and the regression coefficient of population mean yields on number of cycles of selection were estimated from a combined analysis over environments and sets.

Joint regression analysis

Environmental index values were calculated as the mean yield across all genotypes within each environment. The combined ANOVA across environments was performed considering the environmental index as a single degree of freedom linear regressor (Eberhart & Russell, 1966). The GEI variance was partitioned into a component due to differences in the regression of genotype yields on environmental index and a component due to deviations from regression. The regression of yield on environmental index was performed separately for each genotype to estimate their regression coefficients (b_i). One-way analyses of variance were performed to determine if cycles differed significantly for mean regression coefficients. Confidence intervals for the coefficient of correlation between b_i and mean yield were estimating following Steel & Torrie (1980).

AMMI analysis

Within each environment, yields of each experimental family and check line ('genotypes') were adjusted for

set effects. The residual sums of squares due to check lines repeated within and across sets from each environment were summed and divided by the summed degrees of freedom for residuals to obtain a pooled estimate of residual error variance. The main effects of genotypes and environments were obtained from a combined analysis of variance across environments using SAS Proc GLM (SAS Institute Inc., 1999). The residuals from this analysis were then treated as a multivariate data set: for each genotype, the GEI residuals from the ten different environments were treated as ten variables measured on the same genotype. Principal components analysis was implemented with SAS Proc PRINCOMP (SAS Institute Inc., 1999) to obtain the eigenvalues and eigenvectors of this GEI residual matrix. To choose the number of principal components to use for the AMMI model, we followed Gauch (1992) in using the minimum number of principal components necessary to account for the 'pattern', as opposed to 'noise', in the GEI variance. The amount of noise in the GEI sum of squares was estimated by multiplying the error mean square by the degrees of freedom for GEI. Scores from the principal components used in the AMMI analysis were calculated for each environment.

Superiority analysis

At each location, the maximum mean yield among all genotypes was noted. Then for each genotype, the mean square difference between its yield and the maximum yield at that environment was calculated. This was repeated for each environment (where different genotypes may represent the maximum in different environments) and the mean square difference between the genotype and the maxima was averaged over environments to compute the superiority index (P_i) (Lin & Binns, 1988). Superiority indices were computed for four different measures of within-location mean yields of each genotype: 1) traditional ANOVA mean, 2) traditional ANOVA mean standardized by subtracting the environment mean and dividing by the standard deviation of genotype means in that environment, 3) AMMI predicted mean (based on first two principal component scores of the AMMI analysis), and 4) AMMI predicted mean standardized in the same manner as in 2. One-way analyses of variance were performed to determine if cycles differed significantly for mean superiority indices.

Correlations between pairs of environments

Phenotypic correlations between mean yields of lines within each cycle in each pair of environments were estimated using SAS Proc CORR (SAS Institute Inc., 1999). Genotypic correlations between environments i and j were estimated as $r_{gij} = r_{pij}/h_i h_j$, where r_{pij} is the phenotypic correlation between the environments and h_i and h_j are the square roots of the line mean heritabilities within each environment (Cooper & DeLacy, 1994).

Partial least squares regression of genotype-by-environment residuals on climate variables

The following climate variables were measured in each testing environment: maximum daily temperature, minimum daily temperature, and daylength. The growing season within each environment was divided into two periods, before and after the mean heading date within the environment. Each of these periods was then divided into two equal periods, resulting in four time periods for each environment: period 1 represented the time from planting to halfway to the mean heading date; period 2 represented the time from the end of period 1 to the mean heading date; period 3 represented the time from the mean heading date until halfway to the harvest date (complete maturity); and period 4 represented the time from the end of period 3 to the harvest date. For each time period and environment, the average maximum and minimum daily temperatures and the average daylength were calculated. Twelve climatic variables resulted: MaxT1, MaxT2, MaxT3, and MaxT4, the average maximum daily temperatures within time periods 1, 2, 3, and 4, respectively; MinT1, MinT2, MinT3, and MinT4, the average minimum daily temperatures within time periods 1, 2, 3, and 4, respectively; and Day1, Day2, Day3, and Day4, the average daylengths within time periods 1, 2, 3, and 4, respectively. Each climatic variable was standardized by subtracting the mean across environments and dividing by the standard deviation of the variable.

Regression of the matrix of standardized genotype-by-environment interaction effects on the matrix of climate variables was performed using partial least squares regression (Aastveit and Martens 1986; Vargas et al., 1998) in SAS Proc PLS (SAS Institute Inc., 1999). The number of latent variables to extract was chosen in the same manner as the number of principal components in the principal components analysis. The

Table 1. Means of agronomic traits of parent lines and each selection cycle, averaged over all environments

Cycle	Yield g m^{-2}	Test weight kg m^{-3}	Heading date dap[1]
Parents	569	484	58.6
C0	573	477	57.5
C1	592	476	57.6
C2	603	468	56.9
C3	624	467	57.9
LSD (0.05)	28	7	0.4
b-value[2] ($year^{-1}$)	16***	–4***	0.1*

[1] Days after planting.
[2] Slope of the regression of population means on cycles (years) of selection.

mean dependant variable weightings (Y-weightings) for each extracted latent variable were computed for each genotype. One-way analyses of variance of the Y-weightings for each latent variable were performed to compute the mean weightings for each cycle population and to test the significance of differences among cycle means.

Results and discussion

Direct and correlated mean responses

Mean grain yield averaged across environments increased by 16 g m^{-2} per cycle of selection (Table 1). Neither above-ground biomass nor plant height changed significantly over cycles of selection. Heading date averaged across environments increased significantly, but by a mere 0.1 days per cycle (Table 1). The heading date responses observed within locations were not consistent, however. Whereas heading date in C3 tended to be later than C0 in Idaho and Norway, no differences among cycles were observed in Iowa. An unfavorable correlated response was observed for average test weight across environments. Test weight decreased significantly by 4 kg m^{-3} per cycle (Table 1), and this response was consistent within all environments.

Genotype-by-environment interaction for grain yield

Holland et al. (2000) reported that genotype-by-environment interactions for yield were significant in this experiment. The GEI variance component was greater than the genotypic variance component within each cycle, ranging from 1.7 (in cycle 2) to 2.5 times (in cycle 0) greater.

Table 2. Mean regression coefficients (b_i) and correlations between regression coefficient and mean yield ($r_{b \cdot yld}$) (and their 95% confidence intervals) for parent lines and each cycle of selection computed from regression of individual genotype yields within environments on mean environmental yields

Cycle	b_i	$r_{b \cdot yld}$
Parents	0.93	0.66 (0.32, 0.85)
C0	0.96	0.66 (0.52, 0.76)
C1	1.00	0.80 (0.72, 0.86)
C2	1.01	0.84 (0.77, 0.89)
C3	1.04	0.83 (0.76, 0.88)
LSD_1 (0.05)[a]	0.05	
LSD_2 (0.05)[b]	0.06	

[a] LSD_1 (0.05) is least significant difference appropriate for comparisons among cycle means.
[b] LSD_2 (0.05) is least significant difference appropriate for comparisons of cycle means and parental mean.

Joint regression analysis

Differences among genotypes for linear regression on environmental index accounted for 41% of the genotype-by-environment interaction variance. Cycles differed significantly for mean regression coefficient (b_i) (Table 2).

The regression coefficient increased significantly by an average of 0.023 per cycle. Eberhart & Rusell (1966) considered a stable genotype to be one with a regression value of 1, high mean yield, and low deviation from regression. The increase of regression values with cycles of selections indicates that selection enhanced the potential for genotypes to respond to more productive environments. Does this mean that the later cycles of selection are less stable, in that they are expected to perform worse in low productivity environments? In the target population of environments for this population – which include Iowa, Norway, and Idaho, this was not so; the later cycles of selection outyielded the original population even in the lower-productivity environments (Holland et al., 2000). The result could be different if more stressful environments were considered, but we have no data to address that situation. In this case it simply means that the absolute rate of yield increases was greater in the higher productivity environments, as shown by Holland et al. (2000). Holland et al. (2000) also found that the

rate of increase as a proportion of the original population mean within the same environment was actually greater in the lowest productivity environment than in the highest productivity environment, however. It is important to stress that the low productivity environments in this experiment were represented by Iowa, and may not be considered by others to be low productivity environments. The definition of stability depends strongly on the range of target environments considered (Ceccarelli, 1989).

Overall, mean yield across all environments was highly positively correlated with the regression coefficient ($r = 0.78$, $p < 0.0001$). We estimated this correlation independently in each cycle and found that the correlation was originally at $r = 0.66$ in C0, and it increased to $r = 0.80$ in C1 and remained above 0.80 in cycles 2 and 3 (Table 2). The correlation was significantly greater in C2 than in C0 at $P = 0.05$ and greater in C3 than in C0 at $P = 0.10$ (Table 2). It seems that selection favored genotypes with greater mean yields and regression coefficients, and created populations in which a high correlation between mean yield and regression coefficient was maintained. This suggests that there was a higher frequency of genotypes with relatively low mean yields and high regression coefficients in the original population that were eliminated in the first cycle of selection. When we regressed standardized yields on environmental index, we found no significant differences among cycles for mean regression coefficients. For all cycles, the regression coefficient of standardized yield on environmental index was very close to zero, indicating that mean standardized yields were very similar in low and high productivity environments within each cycle.

Superiority analysis

Significant differences among cycles were observed for superiority parameters in all cases, whether they were based on ANOVA or AMMI estimates or standardized or unstandardized yields. Superiority parameters decreased consistently with each cycle of selection (Table 3). Decreasing values of P_i indicate increasing adaptability of each cycle (Lin and Binns 1988). We estimated the correlations between superiority indices and mean yields for each method and found very large negative correlations for each method that were consistent across cycles. Over all cycles, the correlations between mean yield and superiority index were $r = -0.96$ for ANOVA yield estimates, AMMI predictions, and standardized AMMI predictions and $r = -0.93$ for standardized ANOVA predictions ($p < 0.0001$ in all cases). This high correlation indicated that the increase in mean yields across environments due to selection was accompanied by reasonably consistent yield increases within each environment, i.e. that improvements in mean yield and general adaptability were made simultaneously. This is congruent with the results reported by Holland et al. (2000).

Relationships among target environments

AMMI analysis was used to reveal similarities among environments, according to similar GEI responses. Approximately 45% of the GEI variance was expected to be due to "noise" and 55% due to "pattern". The first two principal components accounted for 56% of the G × E variation, and so were included in the AMMI model. The first principal component primarily separated the Idaho and Norway environments from the Iowa environments and accounted for 45% of the GEI variation (Figure 1). The second principal component tended to separate the environments according to year, with very little weight placed on either Kanawha environment, and accounted for an additional 11% of the variation (Figure 1). The first principal component was significantly correlated with mean environment yield ($r = -0.79$, $p = 0.006$), while the second principal component was not significantly related to mean environment yield (Figure 1).

Holland et al. (2000) demonstrated that the selection program based on yield evaluations in diverse environments enhanced mean yields across environments as well as yields within each environment. In this analysis, we tested the hypothesis that this program also resulted in altered genetic correlations among grain yield pairs of target environments. Three striking responses were observed when correlations between yield in pairs of environments were compared between cycle 0 and cycle 3. First, the correlations between yield in different years at the same location decreased in the later cycle population (Table 4). Second, seven of eight of the correlations between Iowa environments and Norway or Idaho environments were greater in cycle 3 than in cycle 0 (Table 4). Third, one environmental pair exhibited a significant negative phenotypic correlation in C0, but no such negative correlations were observed in cycle 3 (Table 4). The improvement in broad adaptation in later cycles was accomplished in part by eliminating negative correlations and strengthening positive correlations between Iowa and the other target locations.

Table 3. Mean grain yield superiority parameters (P_i) for each cycle of selection based on four different within-environment yield estimations

Cycle	Superiority parameter (P_i)			
	ANOVA estimates	Standardized ANOVA estimates	AMMI predictions	Standardized AMMI predictions
P	940	11.6	255	12.3
0	875	11.2	231	11.1
1	808	10.5	206	9.9
2	750	9.3	173	8.3
3	668	8.5	139	6.7
LSD_1 (0.05)[a]	86	0.9	33	1.6
LSD_2 (0.05)[b]	105	1.0	41	2.0

[a] LSD_1 (0.05) is least significant difference appropriate for comparisons among cycle means.
[b] LSD_2 (0.05) is least significant difference appropriate for comparisons of cycle means and parental mean.

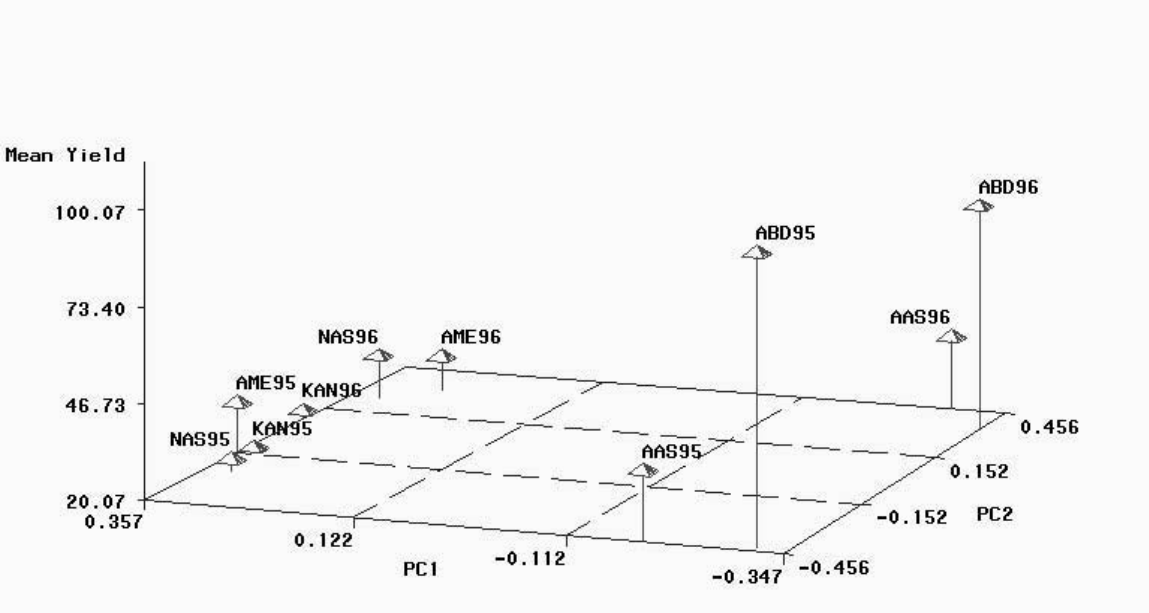

Figure 1. Testing environments plotted against first two principal components of GEI effects from AMMI analysis (horizontal axes) and mean yield (vertical axis). Environments are designated as follows: AAS95 = Ås, 1995; AAS96 = Ås, 1996; ABD95 = Aberdeen, 1995; ABD96 = Aberdeen, 1996; AME95 = Ames, 1995; AME96 = Ames, 1996; KAN95 = Kanawha, 1995; KAN96 = Kanawha, 1996; NAS95 = Nashua, 1995; NAS96 = Nashua, 1996.

Differential genotypic responses to Iowa compared to Norway or Idaho contributed most to the GEI variance (Figure 1), therefore, improved genetic correlations between these locations was most important for increasing the average genetic correlation among environments reported by Holland et al. (2000). The offsetting reduction in specific adaptation (decrease in correlations between years within a location, Table 4) was of minor concern because mean yield increased within all locations, averaged over years.

Climate effects on genotype-by-environment interactions

Aberdeen had the greatest mean maximum daily temperatures within each time period of the growing season, but also had the lowest mean minimum daily

Table 4. Genotypic (above diagonal) and phenotypic (below diagonal) correlations among line grain yields in different evaluation environments by cycle of selection

	Ås, 1995	Ås, 1996	Aberdeen, 1995	Aberdeen, 1996	Iowa, 1995	Iowa, 1996
Cycle 0						
Ås, 1995		0.68	0.95	0.84	0.15	0.35
Ås, 1996	0.42***		0.54	0.69	–0.42	–0.04
Aberdeen, 1995	0.49***	0.34***		0.78	0.35	0.52
Aberdeen, 1996	0.52***	0.53***	0.49***		0.04	0.25
Iowa, 1995	0.09	–0.32***	0.22*	0.03		0.92
Iowa, 1996	0.19	–0.03	0.29**	0.17	0.61***	
Cycle 1						
Ås, 1995		1.00	1.00	0.87	0.09	0.06
Ås, 1996	0.67***		0.80	0.87	–0.19	–0.17
Aberdeen, 1995	0.64***	0.54***		0.83	0.30	0.35
Aberdeen, 1996	0.51***	0.64***	0.57***		–0.05	0.09
Iowa, 1995	0.05	–0.13	0.19	–0.03		0.88
Iowa, 1996	0.03	–0.11	0.21*	0.06	0.54***	
Cycle 2						
Ås, 1995		0.79	0.92	0.84	0.17	0.08
Ås, 1996	0.58***		0.91	0.81	0.03	–0.06
Aberdeen, 1995	0.61***	0.63***		0.92	0.45	0.29
Aberdeen, 1996	0.62***	0.62***	0.64***		0.38	0.24
Iowa, 1995	0.10	0.02	0.25**	0.19		1.00
Iowa, 1996	0.04	–0.03	0.13	0.12	0.43***	
Cycle 3						
Ås, 1995		0.72	0.87	0.74	0.47	0.57
Ås, 1996	0.46***		0.58	0.82	0.02	0.51
Aberdeen, 1995	0.49***	0.41***		0.69	0.56	0.42
Aberdeen, 1996	0.46***	0.63***	0.47***		0.12	0.54
Iowa, 1995	0.22*	0.01	0.29**	0.07		0.28
Iowa, 1996	0.27**	0.30**	0.22*	0.31**	0.12	

*, **, *** Significant at P = 0.05, 0.01, and 0.001 probability levels, respectively.

Table 5. Climate data from each testing environment used for partial least squares regression of genotype-by-environment interaction effects on climate variables

Environment	Variable											
	MaxT1	MaxT2	MaxT3	MaxT4	MinT1	MinT2	MinT3	MinT4	Day1	Day2	Day3	Day4
						C°						
Ås, 1995	14.4	19.1	22.3	22.9	5.8	9.8	11.8	10.8	1063	1116	1046	925
Ås, 1996	16.3	18.1	21.0	23.1	6.7	9.5	9.0	12.7	1099	1110	1030	914
Aberdeen, 1995	21.0	27.0	30.1	30.1	6.8	8.8	8.1	7.5	912	913	873	821
Aberdeen, 1996	23.8	28.1	30.6	30.9	6.0	7.6	9.2	6.5	909	918	887	829
Ames, 1995	16.2	26.2	25.6	29.9	6.5	14.6	15.2	18.5	858	909	908	889
Ames, 1996	17.6	21.1	28.7	27.9	3.4	11.2	18.3	16.5	826	894	913	896
Kanawha, 1995	18.7	27.1	28.9	29.8	6.1	15.2	15.9	16.3	868	916	912	891
Kanawha, 1996	18.6	23.5	29.6	28.0	5.7	12.5	15.8	14.5	861	913	915	885
Nashua, 1995	17.8	26.4	27.3	28.2	6.4	14.5	15.5	16.0	865	915	913	892
Nashua, 1996	13.9	21.2	28.1	26.3	2.5	10.6	16.0	13.8	839	905	919	896

Table 6. Independent variable loadings (X-loadings) of first three latent variables from partial least squares regression of genotype-by-environment interaction effects on climatic variables

Climate variable	x_1	x_2	x_3
MaxT1	0.30	–0.28	0.10
MaxT2	0.06	–0.35	0.32
MaxT3	0.00	–0.37	–0.22
MaxT4	0.01	–0.39	0.14
MinT1	0.24	0.00	0.71
MinT2	–0.41	–0.07	0.45
MinT3	–0.49	–0.06	–0.13
MinT4	–0.48	0.03	0.21
Day1	0.28	0.32	0.17
Day2	0.18	0.37	0.12
Day3	0.05	0.39	0.06
Day4	–0.30	0.32	0.04
Percent of climatic variation explained	31.7%	51.9%	12.6%

Table 7. Mean genotypic Y-loadings of each selection cycle and parents for first three latent variables of partial least squares regression of genotype-by-environment interaction effects on climatic variables

Cycle	x_1	x_2	x_3
Parents	–0.021	0.005	0.013
C0	–0.011	0.000	0.016
C1	0.002	0.011	0.005
C2	–0.003	–0.008	0.001
C3	0.011	–0.008	–0.015
LSD_1 $(0.05)^a$	0.013	0.013	0.013
LSD_2 $(0.05)^b$	0.023	0.023	0.023
Percent of GEI variation explained	34.7%	12.8%	5.3%

temperatures within the last three time periods each year (Table 5). Ås had the lowest mean maximum daily temperatures in all growing periods and the longest daylengths (Table 5). The Iowa environments tended to have the greatest mean minimum daily temperatures and the shortest daylengths (except for the final growing period) (Table 5). It was not possible to include precipitation as a climate variable because the evaluation trials in Norway and Idaho were irrigated, whereas the trials in Iowa were not.

Three latent variables extracted using the partial least squares regression procedure explained a total of 96.2% of the variation in standardized climate data (Table 6) and 52.8% of the GEI variance (Table 7). The first latent variable (x_1) explained 31.7% of the climate data variation (Table 6) and 34.7% of the genotype-by-environment interaction variance (Table 7). This factor primarily represented the maximum and minimum temperatures and the daylength in the first growing period (MaxT1, MinT1, and Day1) contrasted with the minimum temperatures in the other three periods and the daylength in the final growing period (Day4), with greatest weight given to negative MinT2, MinT3, and MinT4 (Table 6). The second factor (x_2) accounted for 51.9% of the climate data variation (Table 6) and 12.8% of the genotype-by-environment interaction variance (Table 7) and represented primarily the average daylength in all periods (Day1, Day2, Day3, and Day4) contrasted with the maximum temperature in all periods (MaxT1, MaxT2, MaxT3, and MaxT4) (Table 6). The third factor, x_3, accounted for 12.6% of the variation in climate data (Table 6) and 5.3% of the genotype-by-environment interaction variance (Table 7). This factor represented mostly the minimum temperatures in the first two growing periods (MinT1, MinT2) and the maximum temperature in the second growing period (MaxT2) (Table 6).

The Y-loadings of each of these three factors was computed for each genotype. The Y-loadings indicate how much weight is given to each factor when optimally estimating a genotype's genotype-by-environment interaction effects in the partial least squares regression procedure. No significant differences among cycles were observed for the Y-loadings of factor x_2 (Table 7), suggesting that selection did not alter the mean interaction between genotypes and this climate factor. In contrast, significant differences were observed among cycles for Y-loadings of factors x_1 and x_3 (Table 7). The mean x_1 loading for C3 was positive and significantly greater than the negative mean loading for C0 (Table 7). The genotype-by-environment interaction effects of genotypes in later cycles of selection were more positive with respect to factor x_1, suggesting that the later cycles of selection tended to respond more positively to greater temperatures and longer daylengths in the earliest growing period, lower temperatures in the other three time periods, and shorter daylengths in the final growing period. This may mean that the later cycle genotypes have less tolerance for heat stress but have greater capacity to respond to early season heat and light and to produce better under cooler daily minimum temperatures during panicle emergence and grain-filling. The mean x_3 loading for C3 was negative and significantly smaller than the positive mean loading for C0 (Table 7). This result suggests that the later cycle populations

responded more favorably to cooler minimum temperatures in the first two growing periods (in partial contrast to the weightings in x_1) and also to cooler maximum temperatures in the growing period preceding heading. Taken together, the results of the partial least squares regression analysis suggest that genotypes in later cycle populations, in addition to their greater mean yields within and across environments, have the capacity to produce greater grain yields under temperatures cooler than the average in the testing environments reported here. The physiological basis for this change is not obvious from these data, although the slightly later heading dates of the later cycles within the Idaho and Norwegian environments may contribute to the ability of later cycle families to capitalize on cooler than average environments by extending the growing and grain-filling developmental stages. The correlated change in heading date overall, however, was very slight (Table 1), and cannot account for a substantial proportion of the more dramatic changes in yield ability and stability.

Conclusions

Oat families developed from recurrent selection for adaptation to diverse environments demonstrated greater mean grain yield within and across environments and greater yield stability as measured by superiority statistics. Clustering environments and analyzing the correlations between pairs of environments provided greater insight into the response of the population to selection in terms of adaptation than did the simpler joint regression and superiority analyses. Genotypic correlations among the most diverse target environments increased in later cycles, offsetting some decreases in correlations between more similar environments, and contributing to the increased mean genetic correlation among all cycles. In addition, the increased stability and mean productivity resulting from selection were accompanied by a shift toward greater productivity in cooler environments.

The only unfavorable response observed in this population was the decline in test weight, which is the primary indicator of grain quality. We suggest that superior lines developed from this population will serve as useful breeding parents in crosses with locally adapted materials in both U.S.A. and Scandinavia.

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